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ON THE INHERITANCE OF SOME CHARACTERS IN WHEAT. I

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I. INTRODUCTION.

THE investigations described in this paper form part of the work undertaken at Pusa during the years 1905 to 1912 in connection with the improvement of Indian wheat. The earlier practical results and those dealing with classification are to be found in former papers. The present account deals only with the information obtained on the laws governing the inheritance of the various characters in wheat and with the gametic factors which are involved in these characters.

The results relating to the red colour of the grain, in which the occurrence of several factors was demonstrated, were obtained some years ago and were about to be published when the admirable investigations of Nilsson-Ehle[1] at Svalöf were made public. This information was in consequence held over until the experiments dealing with bearding and felting could be included. The results obtained at Pusa both confirm and extend the work of Nilsson-Ehle

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1 Nilsson-Ehle, *Kreuzungsuntersuchungen an Hafer und Weizen*, Lund, 1909; *Kreuzungsuntersuchungen II*, Lund, 1911.

as to the complex nature of the characters in wheat and the existence of more than one factor in characters which to the eye appear simple.

Nilsson-Ehle, starting from the standpoint of Bateson's presence and absence hypothesis, has obtained very interesting results at Svalöf. He bases his conclusions on a study of wheat and oats, and the characters investigated in wheat were chaff colour, grain colour, ear form and resistance to yellow rust. His conclusions are summed up in the following paragraphs :—

1. Characters which to the eye appear simple, for example, the red colour of the grain or chaff, may be complex and may contain two or more factors. These factors may exist independently and each produces by itself a red colour and thus the red colour in chaff or grain, even when simple, is not always due to the same factor. When two red wheats are crossed, each containing several red factors, one of which is common to both, the result, in the second generation, is a series of red tones which, although distinct, defy accurate classification. Thus when the factors are numerous, and the differences between them are small, a continuous series of forms would result in the F_2.

2. In the mode of inheritance there is no inherent difference between qualitative and quantitative characters. In such quantitative characters as resistance to rust or length of the internodes of the rachis the behaviour of the various generations from the cross indicate the existence of several factors. The difficulty in dealing with the inheritance of physiological characters such as rust resistance and with characters concerned with size is the want of an analyser, that is, a wheat in which the particular character is totally absent. In studying the inheritance of red colour factors, a white wheat acts as an analyser. It is, however, impossible to use a wheat without height or size in investigating characters dealing with the dimensions of organs. Similarly, there is no absolutely rust resistant wheat which can act as an analyser for the study of the factors involved in this character. Both qualitative and quantitative characters may be complex and may be made up of several factors which are inherited independently.

3. The influence of environment is of considerable importance in the study of inheritance when the factors differ from each other by small amounts. The number of homozygotic forms which are possible is expressed by the formula 2^n, where n is the number of factors. Thus, if there are four factors, 16 homozygotic forms are possible. It is obvious that when the total number of factors in any one character is large the types of wheat will differ from each other very slightly. Nevertheless these differences will be inherited. In studying this inheritance, however, environmental differences supervene, and these latter may be greater than the inherited differences. For example, in the study of inheritance of height in wheat the environmental differences may be greater than and so mask the inherited variations.

4. The existence of so many factors and the occurrence of natural crossing[1] [2] [3] are sufficient to account for the complexity of botanical varieties in wheat and for the existence of a large number of types which breed true and which differ from each other very slightly. Even a small number of factors by recombination among themselves is sufficient to produce a large number of types. Many of the characters of wheat have already been shown to owe their existence to several factors. Further work will doubtless increase the number of these factors. (In the investigations described in the present paper relating to felted and smooth chaff and to bearded and beardless wheats it is shown that at least four and possibly more factors are involved in each of these characters.) The various combinations of these factors among themselves would give a relatively enormous number of different wheats.

5. The complexity of the characters in wheat renders it more than ever necessary that all studies in inheritance should be made with pure lines, that is, with cultures grown from a single parent plant. Such cultures, however, even if they breed true in all visible characters, may not necessarily be homozygotic, especially in physiological characters. In the present state of knowledge,

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[1] Kiessling, *Fühling's land. Zeitung*, Bd. 57, 1908, s. 737.
Nilsson-Ehle, *l.c.*, 1909, s. 16.

[3] Howard and Howard, *Mem. Dept. Agr. in India* (Bot. series), Vol. III, No. 6, 1910.

however, pure lines are the best material available for the work.

Three series of crosses with Indian wheats are involved in the investigations described in this paper, and in all cases the work was started from pure lines. The first was made at Lyallpur in 1907 between various pure lines of Punjab wheats. The first and second generations of these crosses were grown at the Cawnpore Experiment Station[1] and the third generation at Pusa. In this series of crosses the F_1 plants of each cross were mixed, while the F_2 and F_3 plants were kept separate and sown and reaped plant by plant. The second series of crosses was made at Pusa with various pure lines obtained from local and other wheats which had been under observation for some years. In this series the F_1 plants were kept separate, so that the full history of each cross can be traced from each cross-fertilized seed. The third series of crosses was made at Cambridge in the summer of 1910, and the F_1 generation was grown partly at Pusa and partly at Cawnpore in the wheat season of 1910-11, while the second generation was grown at Pusa in 1911-12. The principal object of this latter series was to cross European and American rust resistant wheats with various Indian lines of high grain quality with the object of securing hybrids of use in India, characterised by higher rust resistance and stronger straw than those at present grown. American Club, which was used by Biffen at Cambridge as a parent resistant to yellow rust, when grown at Pusa proved to be very rust resistant under Indian conditions, although it was a late form and did not complete its growth period till well into the hot weather when forms like Einkorn are always attacked by black rust (*P. graminis*) sooner or later. Its late period of maturity prevented any crossing with Indian wheats at Pusa, so it was decided to attempt the work at Cambridge where the Indian parents were sown for us by Professor Biffen as spring wheats in 1910. The Indian wheats developed very feebly under English conditions, but sufficient pollen was

[1] For facilities at the Cawnpore Experiment Station we take this opportunity of acknowledging our indebtedness to Mr. H. Martin Leake, Economic Botanist to the United Provinces.

obtained for crossing on to various English and American parents, such as American Club and Red Fife. We take this opportunity of expressing our thanks to Professor Biffen for facilities given for the hybridization work at Cambridge and for the sowing and care of the Indian cultures in 1910.

In the conduct of hybridization work on wheat under sub-tropical conditions several difficulties have to be overcome which are not experienced in Europe and America. At Pusa, wheats have to be grown on the moisture stored up in the subsoil during the previous monsoon and the rainfall after sowing time is insignificant and may be nothing at all. All the generations have to be raised as a dry crop, and the sowing must be carried out without loss of moisture. Irrigation tends to prolong the growth period of plants sown singly and to bring on rust. Any lengthening of the growth period of wheat is a great disadvantage in India as the plants are bound to be dried up by the hot winds before ripening can take place. The great difficulty is to grow the single seeds under conditions comparable with those obtaining in a field crop. For this it is necessary that the seed should be sown at the proper depth and the soil consolidated afterwards. Dibbling in the seed or sowing in furrows made by hand ploughs is not satisfactory as the plants do not root properly and do not stand up during the windy weather previous to harvest. Such plants also seem to develop a shallow root-system and require a considerable amount of irrigation water to maintain them. The best method so far found is to sow the seeds singly in furrows made by the plough, to cover them by hand and to consolidate the soil by a roller. This results in well rooted plants, but the disadvantage of too much space for each plant and consequently the prolongation of the growth period into the hot weather, with the practical certainty of black rust and premature ripening, still remains. Until the various hybrids forms are fixed and sufficient seed has been obtained for a plot sown in the ordinary manner, it is impossible to say with certainty how they will behave under field conditions. Consequently hybridization work in India involves a very considerable amount of work in the testing of the new forms in plots.

Another disadvantage in India concerns the examination and storage of the harvest. The wheat season is followed shortly by the monsoon when the damp hot air speedily spoils the wheat and brings on the conditions under which its complete destruction by weevils and moths is only a matter of a very few days. It is not possible therefore to work on the material of the previous harvest after June 1st, so that it frequently happens that the material of one harvest cannot be worked through before sowing time comes round. The crop therefore may have to be stored in safely over at least two monsoons. This is done by putting away the bundles of ears of the single plants, when thoroughly dried, in air-tight iron cylinders where they can be kept at least three years without damage or loss of germinating power.

India, however, possesses one great advantage in this work, namely, cheap labour. The cost is only about ten per cent. of that of Europe, so that it is a simple matter to conduct the work on a large scale and to sow and reap at least 1,000 plants of each cross in the second generation. It will be seen that in crosses in which one parent contains a three factor character, this number is by no means excessive if the inheritance is to be worked out in anything approaching thoroughness.

II. FELTED AND SMOOTH CHAFF.

THE inheritance of the felting of chaff in wheat has not previously been worked out in any great detail. Biffen[1] states in regard to this character "The felted or velvety character is dominant, the glabrous recessive." In many cases the 3 : 1 ratio was obtained in the F_2, but in the case of Rivet crosses a series was met with in the F_1 and a ratio of 223 : 116 in the F_2. In the F_3, however, the splitting was simple. Tschermak[2], in a more recent account, states that felting of the glumes prevails over smoothness, but that in many crosses the F_1 is plainly intermediate and the splitting in the second generation is an impure one in which the various stages of felting stand to smooth in the ratio 3 : 1. In one case, where Rivet bearded was crossed with Saxon red, Rimpau mentions the total disappearance of felting in the hybrid. Pitsch[4] found in Felted Essex × felted *Rouge inversable* some smooth progeny in the F_2. The Svalöf results agree with the Mendelian scheme and ratios of 2·7 to 1, 3·7 to 1 and 2·8 to 1 were obtained. In all cases the first generation was felted and in one case in the second generation of smooth Svalöf Extra Square head crossed with a felted wheat one intermediate plant was found.

COMPLEX FELTING.

In this section cases are dealt with in which the felting is due to more than one factor. The first four crosses with a felted wheat were made at Lyallpur in 1907 and in all cases a pure line selected from Punjab Type 9, a red wheat with densely felted chaff, was employed as one of the parents. This was chosen on account of its high yielding power and strength of straw while the other parents

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[1] Biffen, *Jour. of Agr. Science*, 1, 1905, p. 24.

[2] Tschermak, *Die Züchtung der land. Kulturpflanzen*, Bd. IV, 1910 : *Zeit. f. d. land. Versuchswesen in Oesterreich*, 1901, s. 1029.

[3] Rimpau, *Land. Jahrbücher*, 1891.

[4] Pitsch, *Deutsche Land. Presse*, 1899.

were white wheats with relatively poor straw. Later, a fifth cross, with the same felted parent, was made at Pusa and the second generation was raised in 1911-12. The five crosses, in each of which the reciprocal was made, were as follows :—

1. Punjab Type 9 (β) × Punjab Type 16.
2. Punjab Type 9 (β) × Mozaffarnagar white.
3. Punjab Type 9 (β) × Punjab Type 25.
4. Punjab Type 9 (γ) × Punjab Type 13.
5. Punjab Type 9 (α) × Line H II $_4$.

α, β γ, denote similar pure lines from Punjab Type 9.

In all these cases the F_1 was intermediate and in the second generation the ratio of felted to smooth was 15 : 1. The felted plants formed a series and there appeared to be every possible gradation between plants like the felted and smooth parents. All that could be done was to group the plants round arbitrary standards, but many cases arose where a plant could, with equal justice, be placed in either of two groups. The ratios, felted to smooth, obtained in the second generation of these crosses are given in the following table :—

TABLE I.

The F_2 generation of crosses between complex felted and smooth parents.

Cross.		No. of plants.	Felted.	Smooth.	Ratio felted to smooth.
Punjab Type 9 (α) ♀ × H II$_4$ ♂	(1)	137	127	10	12·7 : 1
,, ,,	(2)	190	176	14	12·6 : 1
,, ,,	(3)	185	171	14	12·2 : 1
H II$_4$ ♀ × Punjab Type 9(α) ♂	(4)	117	108	9	12·0 : 1
,, ,,	(5)	175	166	9	18·4 : 1
Total		804	748	56	13·4 : 1
Punjab Type 9(β) ♀ × Punjab Type 16 ♂	(a)	601	562	39	14·4 : 1
,, ,,	(b)	587	550	37	14·8 : 1
Punjab Type 9(β) ♀ × Moz. White ♂	(a)	708	658	50	13·2 : 1
,, ,,	(b)	442	411	31	13·2 : 1
Punjab Type 9(β) ♀ × Punjab Type 25 ♂	(a)	1,017	961	56	17·1 : 1
,, ,,	(b)	603	567	36	15·7 : 1
Punjab Type 9(γ) ♀ × Punjab Type 13 ♂		965	917	48	19·1 : 1
Total of all crosses with Type 9		5,727	5,374	353	15·2 : 1
Expectation			*5,366*	*361*	

a and b denote the numbers obtained by different observers

These numbers suggested the existence of two factors in the felted parent and on examination under the binocular dissecting microscope it was observed that the hairs on the chaff of the felted parent were of two kinds—long silky and short hairs. The intermediate first generation showed on examination under the microscope that both kinds of hairs were present, but both were diminished in length and in density. From the fact that the ratio 15 : 1 was obtained in the F_2 in all the crosses with smooth chaffed wheats and from the appearance of the F_1 generation it appeared probable that these two sorts of hairs were each due to a single factor and were inherited independently. In this case, on Bateson's presence and absence hypothesis, denoting the long factor by L L and the short factor by S S the scheme up to the F_2 generation would be represented by the following :—

S S L L × s s l l ... ... *Parents.*

S s L l ... ... *First generation.*

S S L L+4 S s L l + 2 S s L L+2 S S L l
+s s L L+2 s s L l+S S l l+2 S s l l+s s l l } *Second generation.*

On this assumption the appearance of these various classes in the F_2 generation and the nature of the progeny in the F_3 would be those shown in the following table :—

F_2	F_3
(1). S S L L both kinds of hairs complete.	Constant like the F_2.
(2). S s L l both sets partly developed as in F_1.	Series like the F_2 with felted to smooth in the ratio 15 : 1.
(3). S s L L long factor complete, short factor partial.	All variously felted (SS LL + 2 Ss LL + ss LL).
(4). S S L l short factor complete, long partial.	All variously felted (SS LL + 2 SS Ll + SS ll).
(5). s s L L long factor only complete, short absent.	Constant like the F_2.
(6). s s L l long factor partial, short absent.	Felted : smooth : : 3 : 1 (ss LL + 2 ss Ll + ss ll).
(7). S S l l short factor only complete, long absent.	Constant like the F_2.
(8). S s l l short factor only partial, long absent.	Felted : smooth : : 3 : 1 (SS ll + 2 Ss ll + ss ll).
(9). s s l l smooth.	Constant like F_2.

Although the existence of the various groups in the F_2 could be demonstrated by means of the binocular microscope it proved impossible to analyse this generation completely without an undoubted

representative of each class as a standard. This portion of the work was therefore deferred and the F_3 was first studied as thoroughly as possible in two of the four crosses—Nos. 2 and 3 in the list on page 8. A very large number of plants in the F_2 were selected by eye as representative of the whole series and in addition all the smooth specimens were grown. All the plants were sown seed by seed and the resulting F_3 cultures were reaped plant by plant. The individuals of each of these F_3 cultures were then examined separately under the microscope. The results obtained in this examination in cross No. 2 are given in detail in tables II to V :—

Table II.

The F_3 generation of a cross between a complex felted and a smooth plant.

Plant No.	Felting in F_2 parent.	No. of plants in F_3.	Felting in the F_3 generation.									
			Long and short hairs complete. SS LL.	Long and short hairs partial. Ss Ll.	Long hairs complete, short partial. Ss LL.	Long hairs partial, short complete. SS Ll.	Long hairs complete. ss LL.	Long hairs partial. ss Ll.	Short hairs complete. SS ll.	Short hairs partial. Ss ll.	Smooth. ss ll.	Ratio.
47	Long hairs complete, short hairs partial (Ss LL).	66	14	...	39	...	13	...	...	...	...	
51	do. ...	57	14	...	28	...	15	...	...	...	...	
128	do. ...	73	17	...	35	...	21	...	...	...	...	
139	do. ...	72	16	...	41	...	15	...	...	...	...	
159	do. ...	68	16	...	39	...	13	...	...	...	...	
191	do. ...	79	20	...	39	...	20	...	...	...	...	
258	do. ...	72	22	...	32	...	18	...	...	...	...	
368	do. ...	70	22	...	34	...	14	...	...	...	...	
392	do. ...	58	17	...	28	...	13	...	...	...	...	
507	do. ...	69	21	...	38	...	10	...	...	...	...	
509	do. ...	100	33	...	53	...	14	...	...	...	...	
586	do. ...	78	23	...	45	...	10	...	...	...	...	
597	do. ...	86	22	...	44	...	20	...	...	...	...	
713	do. ...	48	12	...	27	...	9	...	...	...	...	
760*	do. ...	62	18	...	31	...	13	...	...	...	...	
789	do. ...	83	21	...	39	...	23	...	...	...	...	
818	do. ...	80	18	...	45	...	17	...	...	...	...	
861	do. ...	70	20	...	34	...	16	...	...	...	...	
863	do. ...	55	16	...	28	...	11	...	...	...	...	
884	do. ...	72	22	...	33	...	17	...	...	...	...	
889	do. ...	77	21	...	44	...	12	...	...	...	...	
911	do. ...	88	23	...	43	...	22	...	...	...		
995	do. ...	53	13	...	27	...	13	...	...	...	...	
	Total ...	1,636	441	...	846	...	349	...	...	...	...	
	Expectation		*409*		*818*		*409*					
152	Long hairs partial, short complete (SS Ll).	98	27	...	...	46	...	...	25	...	...	
272	do. ...	74	22	...	...	39	...	...	13	...	...	
338	do. ...	73	15	...	...	39	...	...	19	...	..	
412	do. ...	74	23	...	...	40	...	...	11	...	...	
579	do. ...	143	46	...	...	81	...	...	16	...	..	
940	do. ...	87	29	...	...	40	...	...	18	...	...	
975	do. ...	95	11	...	...	53	...	...	31	...	...	
	Total ...	644	173	...	...	338	...	...	133	...	...	
	Expectation		*161*			*322*			*161*			
9	Long hairs complete (ss LL).	67	...	...	...	...	67	...	...	...	...	Uniformly felted.
39	do. ...	all	...	...	...	...	all	...	...	...	...	,,
65	do. ...	75	...	...	...	...	75	...	...	...	...	,,
185	do. ...	65	...	...	...	...	65	...	...	...	...	,,
681	do. ...	79	...	...	...	...	79	...	...	...	...	,,
724	do. ...	76	...	...	...	...	76	...	...	...	...	,,
771	do. ...	105	...	...	...	...	105	...	...	...	...	,,
	Total ...	467	...	...	...	...	467	...	...	...	...	...
	Expectation						*467*					

Table III.

The F_3 generation of a cross between a complex felted and a smooth plant.—(Continued.)

Plant No.	Felting in F_2 generation.	No. of plants F_3.	Felting in the F_3 generation.									
			Long and short hairs complete. SS LL.	Long and short hairs partial. Ss Ll.	Long hairs complete, short partial. Ss LL.	Long hairs partial, short complete. SS Ll.	Long hairs complete. ss LL.	Long hairs partial. ss Ll.	Short hairs complete. SS ll.	Short hairs partial. Ss ll.	Smooth. ss ll.	Ratio felted to smooth.
10	Long hairs partial (ss Ll).	77	...	...	...	...	21	37	...	...	19	3·1 : 1
16	do. ...	88	...	...	...	...	19	42	...	...	27	2·3 : 1
44	do. ...	77	..	...	...	...	20	43	...	...	14	4·5 : 1
45	do. ...	81	...	...	...	...	18	41	...	...	22	2·7 : 1
53	do. ...	69	...	...	...	...	28	32	...	...	9	6·7 : 1
150	do. ...	73	...	...	...	...	18	40	...	...	15	3·9 : 1
193	do. ...	69	...	...	...	...	20	31	...	...	18	2·8 : 1
211	do. ...	88	...	...	...	...	23	39	...	...	26	2·4 : 1
218	do. ...	77	...	...	...	...	19	34	...	...	24	2·2 : 1
256	do. ...	97	...	...	...	...	24	49	..	...	24	3·0 : 1
285	do. ...	73	...	..	...	...	19	39	..	...	15	3·9 : 1
426	do. ...	89	...	...	...	...	22	41	...	...	26	2·4 : 1
485	do. ...	133	...	...	...	...	41	53	...	...	39	2·4 : 1
488	do. ...	110	...	...	...	...	25	56	...	...	29	2·8 : 1
510	do. ...	114	...	...	...	...	32	51	...	...	31	2·7 : 1
523	do. ...	78	...	...	...	...	22	37	...	...	19	3·1 : 1
589	do. ...	108	...	...	...	...	17	60	...	...	31	2·5 : 1
590	do. ...	81	.	...	...	...	22	38	...	...	21	2·9 : 1
592	do. ...	92	...	...	...	...	34	38	...	...	20	3·6 : 1
599	do. ...	69	..	...	...	...	12	34	...	...	23	2·0 : 1
605	do. ...	94	...	...	...	...	22	44	...	...	28	2·4 : 1
632	do. ...	95	...	...	...	...	26	42	...	...	27	2·5 : 1
636	do. ...	82	...	...	...	...	17	37	...	...	28	1·9 : 1
666	do. ...	128	...	...	...	...	30	68	...	...	30	3·3 : 1
698	do. ...	86	...	.	...	...	22	44	...	...	20	3·3 : 1
707	do. ...	70	...	...	...	...	19	36	...	...	15	3·7 : 1
726	do. ...	115	...	...	...	...	25	54	...	...	36	2·2 : 1
733	do. ...	69	...	...	...	...	22	36	...	.	11	5·3 : 1
739	do. ...	124	...	...	...	...	36	59	...	...	29	3·3 : 1
791	do. ...	71	...	...	...	...	15	41	...	...	15	3·7 : 1
831	do. ...	88	...	...	...	...	23	45	...	...	20	3·4 : 1
833	do. ...	118	...	...	...	...	22	61	...	...	35	2·4 : 1
854	do. ...	102	...	...	...	...	31	49	...	...	22	3·6 : 1
873	do. ...	90	...	...	...	...	27	46	...	.	17	4·3 : 1
892	do. ...	140	...	...	...	...	39	75	...	...	26	4·4 : 1
948	do. ...	117	...	...	...	...	24	62	...	...	31	2·5 : 1
965	do. ...	108	...	...	...	...	25	54	...	...	29	2·7 : 1
969	do. ...	68	...	...	...	...	13	33	...	...	22	2·1 : 1
983	do. ...	97	...	...	...	...	22	47	...	...	28	2·5 : 1
985	do. ...	63	...	...	...	...	20	33	..	...	10	5·3 : 1
1004	do. ...	113	...	...	...	...	30	61	...	...	22	4·1 : 1
	Total ...	3,781	..	...	..	...	966	1,862	...	...	953	2·97 : 1
	Expectation						*945·25*	*1890·5*			*945·25*	

Table IV.

The F_3 generation of a cross between a complex felted and a smooth plant.—(Continued.)

Plant No.	Felting in F_2 parent.	No. of plants in F_3	Felting in the F_3 generation.									
			Long and short hairs complete. SS LL.	Long and short hairs partial. Ss Ll.	Long hairs complete, short partial. Ss LL.	Long hairs partial, short complete. SS Ll.	Long hairs complete. ss LL.	Long hairs partial. ss Ll.	Short hairs complete. SS ll.	Short hairs partial. Ss ll.	Smooth. ss ll.	Ratio felted to smooth.
30	Short and long hairs partial (Ss Ll).	93	9	24	12	9	11	6	4	12	6	14·5 : 1
60	do. ...	87	4	25	14	14	4	7	5	6	8	9·9 : 1
257	do. ...	80	5	21	8	13	8	6	5	8	6	12·3 : 1
267	do. ...	86	7	27	12	11	6	9	6	6	2	42·0 : 1
317	do. ...	85	7	20	15	9	5	10	2	10	7	11·1 : 1
401	do. ...	90	6	26	13	12	5	9	8	7	4	21·5 : 1
406	do. ...	71	6	19	9	11	5	7	7	4	3	22·6 : 1
803	do. ...	66	5	19	7	7	6	10	2	7	3	21·0 : 1
867	do. ...	84	8	20	15	11	6	7	7	6	4	20·0 : 1
931	do. ...	89	6	23	11	9	7	11	5	12	5	16·8 : 1
	Total ...	831	63	224	116	106	63	82	51	78	48	16·3 : 1
	Expectation		*51·9*	*207·6*	*103·8*	*103·8*	*51·9*	*103·8*	*51·9*	*103·8*	*51·9*	
31	Short and long hairs partial (Ss Ll).	90	...	...	...	...	...	...	...	...	5	17·0 : 1
59	do. ...	98	...	...	...	...	...	...	...	...	7	13·0 : 1
174	do. ...	83	...	...	...	...	...	...	...	...	3	26·7 : 1
201	do. ...	80	..	...	...	...	...	...	...	...	5	15·0 : 1
232	do. ...	93	...	...	...	...	...	...	...	...	6	14·5 : 1
319	do. ...	81	...	...	...	...	...	...	...	...	6	12·5 : 1
320	do. ...	91	...	...	...	...	...	...	...	...	3	29·3 : 1
330	do. ...	57	..	...	...	...	...	...	...	...	7	7·1 : 1
367	do. ...	79	...	...	...	...	...	...	...	...	8	8·9 : 1
388	do. ...	120	...	...	..	...	...	...	...	...	1	119·0 : 1
405	do. ...	73	...	...	...	...	...	...	...	...	5	13·6 : 1
459	do. ...	74	...	...	...	...	...	...	...	...	8	8·3 : 1
462	do. ...	89	...	...	...	...	...	...	...	...	8	10·1 : 1
470	do. ...	122	...	...	...	...	...	...	...	...	8	14·2 : 1
499	do. ...	87	...	...	...	...	...	...	...	...	11	6·9 : 1
537	do. ...	54	...	...	...		...	...	...	...	3	17·0 : 1
541	do. ...	97	...	...	...		...	...	...	...	6	15·1 : 1
544	do. ...	52	...	...	...	...	...	...	...	...	8	5·5 : 1
581	do. ...	80	...	...	...	...	...	...	...	...	9	7·9 : 1
593	do. ...	92	...	...	...	...	...	...	...	..	4	22·0 : 1
611	do. ...	139	...	...	..	...	...	...	...	...	6	22·2 : 1
624	do. ...	51	...	...	...	...	...	...	...	..	2	24·5 : 1
671	do. ...	92	...	...	...	...	...	...	...	...	4	22·0 : 1
816	do. ...	74	...	...	...	..	...	...	...	...	8	8·5 : 1
838	do. ...	94	...	...	...	...	...	...	...	...	11	7·5 : 1
841	do. ...	79	...	...	...	...	...	...	...	...	5	14·8 : 1
894	do. ...	101	...	...	...	...	...	...	...	...	4	24·2 : 1
906	do. ...	93	...	...	...	..	...	...	...	...	6	14·5 : 1
923	do. ...	129	...	...	...	..	...	...	...	...	7	17·4 : 1
953	do. ...	117	...	...	...	...	...	...	...	...	9	12·0 : 1
960	do. ...	97	...	...	...	...	...	...	...	...	4	23·2 : 1
982	do. ...	77	...	...	...	...	...	...	...	...	7	10·0 : 1
1000	do. ...	112	...	...	...	...	...	...	...	...	8	13·0 : 1
1014	do. ...	93	...	..	...	...	...	...	...	...	7	12·3 : 1
1019	do. ...	41	...	...	...	...	...	...	...	...	5	7·2 : 1
	Total ...	3,912	...	...	...	...	...	...	...	...	292	13·9 : 1
	Expectation										*244·5*	

Table V.

The F_3 generation of a cross between a complex felted and a smooth plant.—(Concluded.)

Plant No.	Felting in F_2 parent.	No. of plants in F_3.	Felting in the F_3 generation.									
			Long and short hairs complete. SS LL.	Long and short hairs partial. Ss Ll.	Long hairs complete, short partial. Ss LL.	Long hairs partial, short complete. SS Ll.	Long hairs complete. ss LL.	Long hairs partial. ss Ll.	Short hairs complete. SS ll.	Short hairs partial. Ss ll.	Smooth. ss ll.	Ratio felted to smooth.
58	Short hairs partial (Ss ll).	82	...	...	...	...	...	...	19	43	20	3·1 : 1
77	do. ...	128	...	...	...	...	...	...	27	77	24	4·3 : 1
114	do. ...	79	...	...	...	...	...	..	14	49	16	3·9 : 1
473	do. ...	105	...	...	...	...	...	...	29	53	23	3·6 : 1
560	do. ...	54	...	...	...	...	...	...	12	29	13	3·1 : 1
651	do. ...	90	...	..	...	...	...	..	18	39	33	1·7 : 1
702	do. ...	72	...	...	...	...	...	...	25	33	14	4·1 : 1
711	do. ...	81	...	...	...	...	...	...	20	37	24	2·4 : 1
728	do. ...	86	...	...	...	...	...	...	19	41	26	2·3 : 1
744	do. ...	55	...	...	...	...	...	...	15	27	13	3·2 : 1
770	do. ...	128	...	...	...	...	...	...	30	65	33	2·9 : 1
796	do. ...	97	...	...	...	...	...	..	26	43	28	2·5 : 1
853	do. ...	65	...	...	...	...	...	...	13	35	17	2·8 : 1
875	do. ...	68	...	...	...	..	...	...	15	32	21	2·2 : 1
922	do. ...	23	...	...	...	...	...	...	6	12	5	3·6 : 1
984	do. ...	121	...	...	...	...	...	...	31	64	26	3·6 : 1
1,026	do. ...	94	...	...	...	...	...	...	25	48	21	3·5 : 1
	Total ...	1,428	...	...	...	...	...	...	344	727	357	3·0 : 1
	Expectation								*357*	*714*	*357*	
15	Short hairs complete (SS ll).	95	...	...	...	...	...	...	95	...	...	Uniformly felted.
233	do. ...	71	...	...	...	..	...	...	71	...	...	,,
243	do. ...	81	...	...	...	...	...	..	81	...	...	,,
260	do. ...	81	...	...	...	...	...	...	81	...	...	,,
373	do. ...	102	...	...	...	...	...	...	102	...	...	,,
665	do. ...	58	...	...	...	...	...	...	58	...	...	,,
787	do. ...	96	...	...	...	...	...	...	96	...	...	,,
968	do. ...	74	...	...	...	...	...	...	74	...	...	,,
	Total ...	658	...	...	...	...	...	...	658	...	...	...
	Expectation								*658*			
67	Short and long hairs complete (SS LL).	99	99	...	...	...	...	...	...	...	...	Uniformly felted.
79	do. ...	112	112	...	...	...	...	...	...	...	...	,,
106	do. ...	104	104	...	...	...	...	...	...	...	...	,,
119	do. ...	103	103	...	...	...	...	...	...	..	...	,,
138	do. ...	99	99	...	...	...	...	...	...	...	...	,,
153	do. ...	?	all	...	...	...	...	...	...	...	...	,,
184	do. ...	63	63	...	...	...	...	..	...	...	...	,,
468	do. ...	77	77	...	...	...	...	...	...	...	...	,,
513	do. ...	?	all	...	...	...	...	...	...	...	...	,,
517	do. ...	?	all	...	...	...	...	...	...	...	...	,,
554	do. ...	66	66	...	...	..	...	...	...	...	...	,,
582	do. ...	91	91	...	...	...	...	...	...	...	...	,,
768	do. ...	103	103	...	...	...	...	...	...	...	...	,,
830	do. ..	81	81	...	...	...	...	...	...	...	..	,,
844	do. ...	81	81	...	...	...	...	...	...		...	,,
959	do. ...	80	80	...	...	...	...	...	...	...	..	,,
973	do. ...	67	67	...	...	...	...	...	...	..	...	,,
990	do. ...	67	67	...	...	...	...	...	...	..	...	,,
	Total ...	1,293	1,293	..	...	...	...	...	...	..	...	...
	Expectation		*1,293*									

It will be seen that the F_3 cultures could be divided into the following classes :—

1. Cultures uniformly and densely felted derived from S S L L.
2. Cultures uniformly and lightly felted derived from s s L L and S S l l.
3. Cultures with all plants felted, but not uniformly, derived from S S L l and S s L L.
4. Cultures with felted and smooth plants in the ratio 15 : 1 derived from S s L l.
5. Cultures with felted and smooth plants in the ratio 3 : 1 derived from S s l l and s s L l.
6. Cultures all smooth.

In dealing with the offspring obtained in the F_3 generation from the various F_2 plants, it was an easy matter to separate classes 4, 5 and 6 from the others and from each other. It was also comparatively simple to separate classes 1, 2 and 3 from each other by the aid of the microscope. By examining a large number of plants in each culture it was not difficult to see whether the felting was uniform or not, and whether one or both kinds of hairs were present. The distinction between the two constituents of class 3, namely, the cultures derived from plants of the gametic constitution S s L L and S S L l was not quite so simple. As was shown on page 9 plants of the constitution S s L L give in the F_3 S S L L +2 S s L L+s s L L (long hairs completely developed), while S S L l gives S S L L+2 S S L l+S S l l (short hairs completely developed). The best means of distinguishing these lies in the well marked difference between plants represented by s s L L and S S l l. Glumes with the long hairs only and complete are easily distinguished under the microscope from those possessing the short hairs only, both by the length and also by the density of the hairs (the long hairs are more sparsely distributed than the short). On this rests the separation of the constituents not only in class 3 but also in class 5. Had the two kinds of hairs been more alike, these classes could not have been subdivided.

It will be seen on examining the tables of the F_3 generation of this cross that the determination of the various classes of felting

involved the microscopic examination of nearly 15,000 plants and that considering the difficulty of the work the numbers obtained correspond very fairly well with expectation. A considerable number of cultures were examined in the class (S s L l), which gave the 15 : 1 ratio, but time did not permit of the detailed examination of more than 831 plants belonging to 10 cultures. The ratio felted to smooth, however, was worked out for 3,912 plants belonging to 35 more cultures. There can be little doubt that had time permitted for the examination of these 3,912 plants they would have confirmed the ten cultures of this class which were worked out in detail.

The complete study of the F_3 generation enabled us to examine the 1,017 plants of the F_2. After the examination of the F_3 it was easy to obtain a representative plant of each of the eight classes of differently felted plants which occurred in the F_2. By mounting a glume of each of these representatives on a slide a set of standards was obtained by the aid of which it was possible to divide the F_2 material into its constituents. A glume of each of the 1,017 F_2 plants was compared with the standards and the class was determined by inspection. The results are given in table VI and it will be seen that the figures obtained compare fairly well with expectation. Even with these standards it was sometimes difficult to determine the proper class to which an individual belonged. For example, in distinguishing plants of the gametic constitution S S l l and s s L l the difference is mainly one of density of the felting, the partially developed long hairs being of almost the same length as the completely developed short ones. A similar difficulty arose with plants represented by S S L L and S s L L.

Table VII.

generation of another cross between complex felted and smooth parents.

No. of ants in F_3.	Felting in the F_3 generation.									
	Long and short hairs complete. SS LL.	Long and short hairs partial. Ss Ll.	Long hairs complete, short partial. Ss LL.	Long hairs partial, short complete. SS Ll.	Long hairs complete. ss LL.	Long hairs partial. ss Ll.	Short hairs complete. SS ll.	Short hairs partial. Ss ll.	Smooth. ss ll.	Ratio.
95	95	...	...	...	...	...	...	...	...	Uniform felted.
95	95	...	...	...	...	...	...	...	...	do.
190	190	...	...	...	...	...	...	...	...	do.
95	...	...	...	...	...	...	...	...	4	22·7
59	...	...	...	...	...	...	...	...	1	58·0
183	...	...	...	...	...	...	...	...	27	5·8
61	...	...	...	...	...	...	...	...	6	9·1
94	...	...	...	...	...	...	...	...	8	10·7
93	...	...	...	...	...	...	...	...	6	14·5
19	...	...	...	...	...	...	...	...	1	18·0
98	...	...	...	...	...	...	...	...	6	15·3
89	...	...	...	...	...	...	...	...	3	28·7
30	...	...	...	...	...	...	...	...	6	4·0
85	...	...	...	...	...	...	...	...	8	9·6
38	...	...	...	...	...	...	...	...	4	8·5
78	...	...	...	...	...	...	...	...	6	12·0
1,022	...	...	...	...	...	...	...	...	86	10·9
									63·9	
100	gave felted progeny only (SS LL, Ss LL and ss LL)						...	...		All felted but not uniform.
44	gave felted progeny only (SS LL, SS Ll and SS ll)						...	...	...	do.
37									...	do.
53									...	do.
80	...	...	...	...	62		...	...	18	3·4 :
83	...	...	...	...	65		...	...	18	3·6 :
163	...	...	...	...	127		...	...	36	3·5 :
					122·25				*40·75*	
37	...	...	...	...	...	...	37	...	...	All uniformly felted.
78	...	...	...	...	...	...	78	...	...	do.
(?)	...	...	...	...	...	...	all	...	...	do.
118	...	...	...	...	...	...	118	...	...	do.
(?)	...	...	...	...	...	...	all	...	...	do.
78	...	...	...	...	...	...	78	...	...	do.
311 + ?	...	...	...	...	...	...	all	...	...	do.
93	...	...	...	...	...	...	74		19	3·9 :
99	...	...	...	...	...	...	69		30	2·3 :
85	...	...	...	...	...	...	66		19	3·5 :
93	...	...	...	...	...	...	68		25	2·7 :
88	...	...	...	...	...	...	66		22	3·0 :
458	...	...	...	...	...	...	343		115	3·0 :
							343·5		*114·5*	

Table VI.

The analysis of the F_2 generation of crosses between complex felted and smooth parents.

Cross.	No. of plants.	Long and short hairs complete. SS LL.	Long and short hairs partial. Ss Ll.	Long hairs complete, short partial. Ss LL.	Long hairs partial, short complete. SS Ll.	Long hairs complete. ss LL.	Long hairs partial. ss Ll.	Short hairs complete. SS ll.	Short hairs partial. Ss ll.	Smooth. ss ll.
Punjab Type 9 ♀ ×										
H II$_4$ ♂	190	13	50	19	19	10		14	28	14
Expectation.		*11·9*	*47·6*	*23·7*	*23·7*	*11·9*	*23·7*	*11·9*	*23·7*	*11·9*
Punjab Type 9 ♀ ×										
Punjab Type 25 ♂	1,017	70	261	115	140	79	107	72	117	56
Expectation.		*63·5*	*254*	*127*	*127*	*63·5*	*127*	*63·5*	*127*	*63·5*
Total	1,207	83	311	134	159	89	130	86	145	70
Expectation.		*75·4*	*301·6*	*150·8*	*150·8*	*75·4*	*150·8*	*75·4*	*150·8*	*75·4*

The cultures of the other cross on Punjab Type 9 which had been continued to the F_3 generation, namely, that on Mozaffarnagar white, were not completely examined owing to want of time. This cross was not dealt with in such detail as in the previous case, but sufficient cultures were examined to show that in this case also the inheritance was the same as in the former. The results are given in table VII:—

The unravelling of the F_2 in the first cross now enabled us to deal with another cross (No. 5 on page 8) in which a pure line from Punjab Type 9 was used as the felted parent. In this case the F_2 material was dealt with direct as the F_3 generation of this cross has not yet been grown. One hundred and ninety F_2 plants were examined under the microscope and the glumes were compared with the set of standards. The numbers obtained are given in the first portion of table VI above, and they are very close to those expected. In this cross the smooth parent was a pure line known as H II_4.

Thus it has been demonstrated that in the case of Punjab Type 9 the felting is composed of two kinds of hairs, each of which can exist separately and is inherited independently of the other.

Another case of complex felting, in which two kinds of hairs are concerned, was met with in the second series of crosses made at Pusa. In this case the felted parent was a pure line from the durum wheat known as Pusa 20, the smooth parent being the line of common wheat known as H III_8. In the F_1 the felting was intermediate, both factors being present, but both reduced in length and density. In the F_2 the figures obtained were 481 felted to 36 smooth pointing to the 15 : 1 ratio. Only 517 plants were grown in the F_2 and the felted individuals formed a series as before. The details so far obtained with this cross are given in the following table :—

Table VIII.

The F_2 generation of a cross between a complex felted durum and a smooth common wheat.

Cross.	No. of plants.	Felted.	Smooth.	Ratio felted to smooth.
Pusa 20 ♀ × H III_8 ♂ (1)	61	58	3	19·3 : 1
,, ,, (3)	119	112	7	16·0 : 1
,, ,, (4)	73	66	7	9·4 : 1
,, ,, (5)	98	90	8	11·3 : 1
H III_8 ♀ × Pusa 20 ♂ (1)	54	50	4	12·5 : 1
,, ,, (2)	59	55	4	13·8 : 1
,, ,, (4)	53	50	3	16·7 : 1
Total	517	481	36	13·4 : 1
Expectation		*484·*	*32·3*	

A marked difference between the short hairs in Pusa 20 and those in Punjab Type 9 was noticed. In this cross in the wheats of the gametic constitution S s l l the short hairs almost disappear and it is only with the greatest difficulty that these forms can be distinguished from those with smooth glumes. This extreme reduction of short hairs in the F_1 was met with again in one of the cases of simple felting referred to below. It would therefore appear probable that the short hairs in Pusa 20 are not due to the same factor as those in Punjab Type 9. It is also improbable, judging by appearance, that the long hairs in both these wheats are identical, the long hairs in Punjab Type 9 being much denser and longer than those in Pusa 20. It is therefore probable that we have four different kinds of hairs, each due to an independent factor and inherited separately, but this can only be proved by further experiments. In Pusa 20 both the kinds of hairs do not differ very widely and it will be much more difficult to analyse the F_2 generation than in the crosses with Punjab Type 9.

Simple Felting.

In two of the parents with felted chaff only one class of hairs was distinguished under the microscope, and in both cases the 3 : 1 ratio was obtained in the F_2. The felted parents in these crosses were lines selected from common wheats and are described in the records as B XI 77 and Pusa 4. The hairs on these wheats, when directly examined, appeared to be different, and this was confirmed by their behaviour in the F_1. In the F_1 from Pusa 4 the same phenomenon as in the crosses on Pusa 20 was observed, namely, the almost total disappearance of the hairs, while in the F_1 from B XI 77 the felting could be seen by the naked eye. If the felting factors in these two wheats are different, a cross between them would give smooth progeny in the F_2. The actual experiment, however, has not yet been carried out. The details of the second generation of the above crosses are given in the following table :—

TABLE IX.

The F_2 generation of crosses between simple felted and smooth parents.

Cross.		No. of Plants.	Felted. Fully.	Felted. Lightly.	Smooth.	Ratio.
BXI 77 ♀ × HI_2 ♂	(1)	194	48	100	46	1 : 2·2 : 1
,, ,,	(2)	227	56	117	54	1 : 2·2 : 1
,, ,,	(3)	233	59	95	79	·7 : 1·2 : 1
HI_2 ♀ × BXI 77 ♂	(5)	253	59	124	70	·8 : 1·8 : 1
TOTAL		907	222	436	249	·9 : 1·8 : 1
			658		249	2·64 : 1
Expectation		...	*226·75*	*453·5*	*226·75*	
			680		*227*	
American Club ♀ × Pusa 4 ♂	(1)	156	32	77	47	·7 : 1·6 : 1
,, ,,	(2)	177	34	95	48	·7 : 2·0 : 1
,, ,,	(3)	195	43	105	47	·9 : 2·2 : 1
,, ,,	(4)	124	27	64	33	·8 : 1·9 : 1
,, ,,	(5)	193	47	98	48	1 : 2·0 : 1
,, ,,	(6)	216	51	109	56	·9 : 1·9 : 1
TOTAL		1,061	234	548	279	·8 : 2·0 : 1
			782		279	2·8 : 1
Biffen's hybrid ♀ × Pusa 4 ♂	(1)	158	37	79	42	·9 : 1·9 : 1
,, ,,	(2)	178	48	88	42	1·1 : 2·1 : 1
,, ,,	(3)	110	26	56	28	·9 : 2·0 : 1
,, ,,	(4)	115	36	47	32	1·1 : 1·5 : 1
,, ,,	(5)	221	55	111	55	1 : 2·0 : 1
,, ,,	(6)	197	49	103	45	1·1 : 2·3 : 1
TOTAL		979	251	484	244	1 : 2·0 : 1
			735		244	3 : 1
Total of both crosses with Pusa 4		2,040	485	1,032	523	
			1,51		523	2·9 : 1
Expectation		...	*1,530*		*510*	

Thus it has been shown that the felting on the chaff of wheat is due to the presence of different kinds of hairs, one or more of which may be present in the same wheat. In all our investigations up to the present each kind of hair has been shown to be due to a single factor and to be inherited independently of any other kind of hair present. The microscopic comparison of the wheats Pusa 20 and Punjab Type 9, and also the breeding experiments make it probable that though each wheat contains two kinds of hairs differing in length, none of the hairs are alike. This gives at least four kinds of hairs and four different factors in two wheats only.

These results led to the examination under the microscope of a large number of other felted wheats, when some interesting observations were made. It was found that the differences in the length and density of the hairs composing the felting are more numerous than would be supposed, and it was found without exception that all densely felted wheats contained two different kinds of hairs, one of which was long and to which was due the densely felted appearance. A large number of macaroni wheats from all over India were examined and in all cases two kinds of hairs were present. With the exception of Pusa 20 and Sindhi of Partabgarh, all the Indian durums examined possess a peculiar long silky tomentose type of hair as well as short hairs. These long hairs are absolutely distinct from the long hairs of Punjab Type 9. As no breeding experiments have been carried out with these wheats, it is impossible to say whether these hairs are intensified forms of other long hairs or whether, as is more probable, they are due to an entirely new factor. In the common wheats examined the felting was found to be simple, but in these cases the different wheats were found to possess hairs of different length. It is probable, in the light of the experience already obtained, that these will be found to be different and to be due to several factors.

As an example of the diversity of the nature of the felted chaff in wheat, the results of an examination of the wheats of the Punjab may be given. In 1908, the wheats of this Province were shown to belong to 25 distinct agricultural types among which there are 8 felted kinds.

Punjab Type 1.[1]	*T. durum*	Two kinds of hairs one short, one very long and silky.
Punjab Type 2.	*T. durum*	Same as Type 1.
Punjab Type 5.	*T. compactum*	Short hairs only.
Punjab Type 8.	*T. vulgare*	Long hairs only, but these are not nearly as long or as silky as those on the macaroni wheats.
Punjab Type 9.	,,	Two kinds of hairs, long and short; the long hairs quite different (shorter and less silky) than those on Types 1 & 2. The long hairs on this type may be the same as those in type 8.
Punjab Type 17.	,,	Long hairs only as in Type 8.
Punjab Type 18.	,,	Short hairs only present, but these are different in appearance to the short hairs present in Type 9.
Punjab Type 19.	,,	Short hairs only present. From their appearance these may be the same as those in Type 9.

The felting of the glumes of wheat is therefore a much more complex character than has hitherto been considered, and the total number of factors involved in this character is considerable and much larger than would be supposed. Considering that a microscopic examination of this character is sufficient to disclose several sorts of hairs, it is surprising the complex nature of felting has not been observed before. Possibly the explanation of this is to be found in the fact that double felting seems to be commoner in macaroni or wheats derived from these than in wheats of the Northern temperate regions where much of the wheat breeding work has been done.

On looking through our collection of European felted wheats two sets of hairs were distinguished in the following Rivet wheats:—

Blé Nonette de Lausanne.
Poulard d' Australie.
Pétanielle noire de Nice.
Blé de miracle.

In all the European common wheats with velvet chaff which we have examined only one set of hairs was observed in any wheat, but the kind of hairs in these wheats was not always the same.

[1] Howard & Howard, *Memoirs of the Dept. of Agr. in India* (Bot. Series), Vol. II, No. 7, 1908.

The only felted common wheat, in which we have so far found two sets of hairs, is Punjab Type 9.

The demonstration of the complex nature of felting is of importance from the systematic point of view. Wheats with different sorts of felting can no longer be placed in the same botanical variety and the present accepted classificatory schemes will need some enlargement. The final unravelling of this character, however, can only be done by breeding experiments a work of some magnitude.

III. GRAIN COLOUR AND CHAFF COLOUR.

Grain Colour.

The inheritance of the red colour in wheat has been investigated in great detail by previous observers. Biffen[1] found that red was dominant over white and obtained the 3 : 1 ratio in the F_2. Tschermak[2] states that red, brown and violet grain colour prevail over white and that after an intermediate F_1 pure and impure splitting in the F_2 takes place in the ratio 3 : 1. Both Tschermak and Nilsson-Ehle found that in certain crosses between red parents white grained individuals were produced in the F_2 thereby showing that the factors in each red parent were not the same. The most detailed investigations on this character are those of Nilsson-Ehle[3] at Svalöf, who in addition to the simple splitting observed by Biffen and others, found ratios of 15 : 1 and 63 : 1 in the F_2, which were proved to be due to the presence of two and three factors respectively in the red parent. Each of these factors was found to be capable by itself of producing the red colour. These red parents with multiple grain colour factors were selected from old country varieties and were found to be exceedingly hardy and to be less liable to sprouting in the ear than white forms.

In our experiments on the inheritance of the red colour of the grain we have found that the F_1 is always red, but the tone of colour is intermediate and lighter than that of the red parent. In the F_2 the following ratios of red to white were obtained.

---

[1] Biffen, *l.c.*

[2] Tschermak, *l.c.*

[3] Nilsson-Ehle, *l.c.*

TABLE X.

The F_2 generation of crosses with single and double red factors in the red parent.

CROSS.	No. of Plants.	GRAIN COLOUR.		RATIO.
		Red.	White.	
Biffen's hybrid ♀ × Pusa 4 ♂ (1)	153	110	43	2·6 : 1
,, ,, (2)	176	140	36	3·9 : 1
,, ,, (3)	109	87	22	3·9 : 1
,, ,, (4)	112	89	23	3·8 : 1
,, ,, (5)	221	179	42	4·2 : 1
,, ,, (6)	195	141	54	2·6 : 1
TOTAL	966	746	220	3·4 : 1
Expectation		*724·5*	*241·5*	
B XI 77 ♀ × H I_2 ♂ (1)	194	139	55	2·5 : 1
,, ,, (2)	227	177	50	3·5 : 1
,, ,, (3)	233	183	50	3·6 : 1
H I_2 ♀ × BXI 77 ♂ (5)	253	190	63	3·0 : 1
TOTAL	907	689	218	3·2 : 1
Expectation		*680·25*	*226·75*	
Punjab Type 9 ♀ (α) H II_4 ♂ (1)	137	119	18	6·6 : 1
,, ,, (2)	189	183	6	30·5 : 1
,, ,, (3)	185	176	9	19·5 : 1
H II_4 ♀ × Punjab Type 9(α) ♂ (4)	117	114	3	38·0 : 1
,, ,, (5)	176	166	10	16·6 : 1
TOTAL	804	758	46	16·5 : 1
Punjab Type 9 (β) ♀ × Punjab Type 16 ♂ (a)	603	567	36	15·7 : 1
,, ,, (b)	567	539	28	19·2 : 1
Punjab Type 9 (β) ♀ × Moz. White ♂ (a)	705	661	44	15·0 : 1
,, ,, (b)	441	403	38	10·6 : 1
Punjab Type 9 (β) ♀ × Punjab Type 25 ♂ (a)	1,020	961	59	16·3 : 1
,, ,, (b)	591	543	48	11·1 : 1
Punjab Type 9 (γ) ♀ × Punjab Type ♂	987	907	80	11·3 : 1
TOTAL of all crosses with Type 9 ...	5,718	5,339	379	14·08 : 1
Expectation ...		*5,360·6*	*357·4*	

TABLE XI.

The F_2 generation of crosses between a three factor red and white parents.

CROSS.	No. of Plants.	GRAIN COLOUR.		Ratio.
		Red.	White.	
American Club ♀ × Pusa 4 ♂ (1)	155	152	3	50·7 : 1
,, ,, (2)	176	170	6	28·3 : 1
,, ,, (3)	195	190	5	38·0 : 1
,, ,, (4)	124	122	2	61·0 : 1
,, ,, (5)	192	187	5	37·4 : 1
,, ,, (6)	216	213	3	71·0 : 1
TOTAL	1,058	1,034	24	43·1 : 1
Expectation		*1,041·5*	*16·5*	
American Club ♀ × Pusa 6 ♂ (1)	132	131	1	131·0 : 1
,, ,, (2)	211	208	3	69·3 : 1
,, ,, (3)	178	175	3	58·3 : 1
,, ,, (4)	97	96	1	96·0 : 1
,, ,, (5)	180	179	1	179·0 : 1
,, ,, (6)	201	199	2	99·5 : 1
TOTAL	999	988	11	89·8 : 1
Expectation		*983·5*	*15·5*	
American Club ♀ × Pusa 22 ♂ (1)	122	117	5	23·4 : 1
,, ,, (2)	165	163	2	81·5 : 1
,, ,, (3)	192	190	2	95·0 : 1
,, ,, (4)	75	69	6	11·5 : 1
,, ,, (5)	147	147	0	147·0 : 0
,, ,, (6)	176	174	2	87·0 : 1
TOTAL	877	860	17	50·6 : 1
Expectation		*863·3*	*13·7*	
TOTAL of all crosses with American Club	2,934	2,882	52	55·4 : 1
Expectation		*2,888·2*	*45·8*	

It will be seen that three distinct kinds of splitting were obtained and that the numbers point to the 3 : 1, 15 : 1 and 63 : 1 ratios. The 15 : 1 ratio was obtained in all the crosses in which Punjab Type 9 was one of the parents thereby indicating the existence of two red factors in the grain colour. The 63 : 1 ratio was observed in all

the crosses in which a pure line of American Club was one of the parents. It will be observed in the figures relating to these ratios that eighteen plants belonging to three crosses were grown in the F_2, that the mean ratio of red to white was 56·4 to 1, and the total number of plants involved was 2,934. Taking the progeny of the F_1 plants separately it will be seen the ratios varied between 11·5 to 1 and 179 : 1, while in one culture all the 147 plants had red grain. The greatest number of plants in any one culture was 216 and the smallest number 75. Compared with these the following figures obtained by Nilsson-Ehle in a similar case are of interest :—

0315 white × Swedish felted red			(a)	F_2	78	red 0	white.
,,	,,	,,	(b)	,,	30	,, 0	,,
,,	,,	,,	(c)	,,	49	,, 0	,,
,,	,,	,,	(d)	,,	31	,, 0	,,
,,	,,	,,	(e)	,,	86	,, 0	,,
,,	,,	,,	(f)	,,	110	,, 0	,,

Investigation of the third generation showed that in reality three red factors were present in the red parent and the F_2 should have given a ratio of 63 : 1 instead of all red plants. The Pusa numbers are undoubtedly better than those quoted from Svalöf, nevertheless it was a mistake to grow only some 200 or so individuals from each F_1 plant. It would have been better to have made a corresponding reduction in the total number of F_1 parents.

In the case of some of the crosses with Punjab Type 9, which gave the 15 : 1 ratio in the F_2, the cultures have been carried on to the third generation and the two red factors isolated. (The crosses in which the 3 : 1 and 63 : 1 ratios were obtained are now being grown in the third generation.) On examining the grain of a large number of the F_2 plants which exhibited the 15 : 1 ratio it was observed that they formed a series and that those with red grain varied in colour from a very light yellowish red to tones as dark as the parent. A similar state of affairs to that observed in the felted chaff of these crosses was therefore obtained, but with the difference that no morphological characters corresponding to the two sets of hairs were present to assist in the unravelling of the series.

A large number of F_2 plants, representative of all the various tones of red in the series, were then sown singly seed by seed and the

resulting harvest examined. These plants gave rise in the F_3 to the following classes :—

1. Cultures in which plants with red and white grain occurred in the ratio 15 : 1.
2. Cultures in which plants with red and white grain occurred in the ratio 3 : 1.
3. Cultures in which all the plants had red grain, the red colour being uniform.
4. Cultures in which all the plants were red grained, but the red colour was not uniform in tone.
5. Cultures in which all the plants were white grained.

The presence of two independent red factors, indicated by the ratio obtained in the F_2, was therefore confirmed by the behaviour of these plants in the F_3.

Representing the two red factors by R_1 and R_2 we therefore get the following scheme :—

Parents $R_1\ R_2 \times r_1\ r_2$

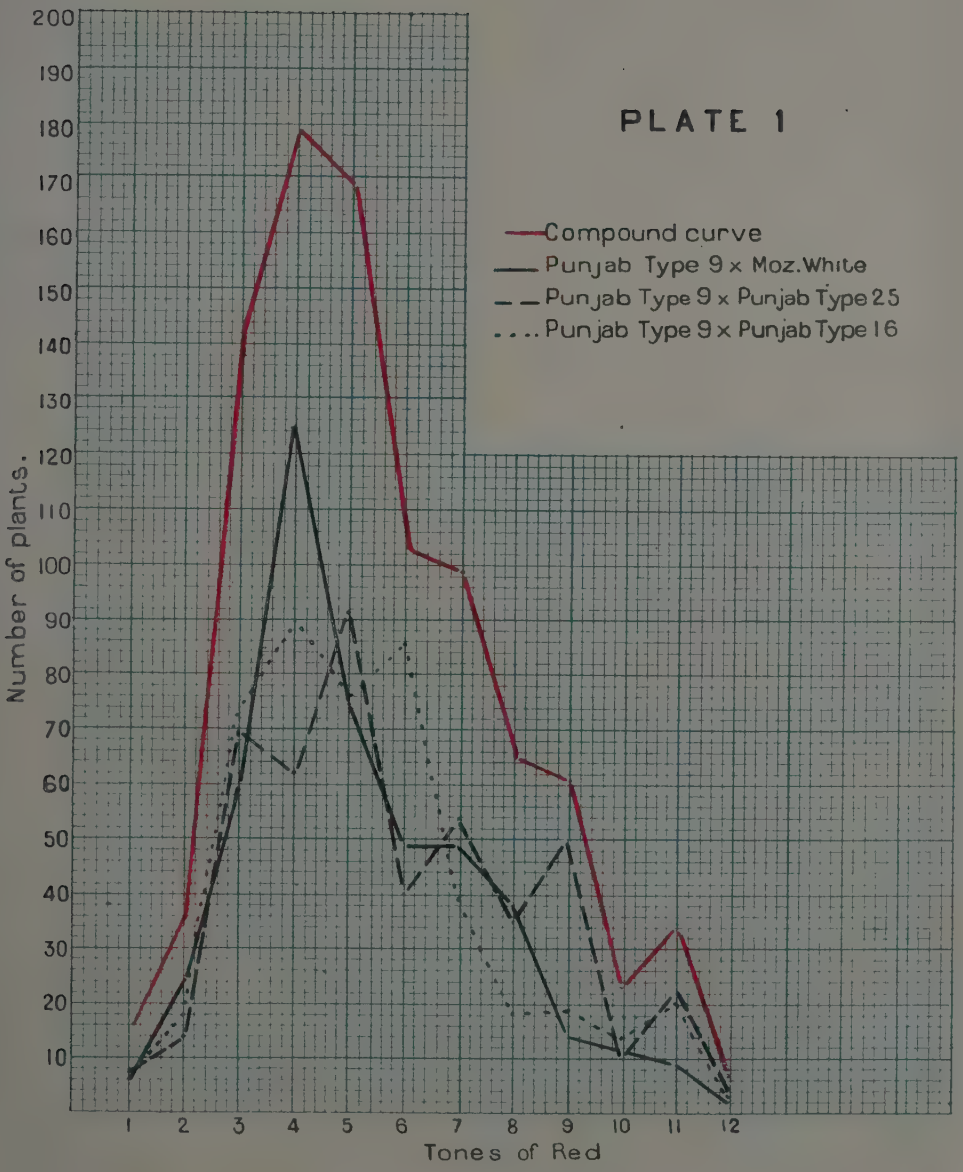
F_1 $R_1\ r_1\ R_2\ r_2$

F_2 $R_1\ R_1\ R_2\ R_2 + r_1\ r_1\ r_2\ r_2 + R_1\ R_1\ r_2\ r_2 + r_1\ r_1\ R_2\ R_2 + 2\ R_1\ r_1\ R_2\ R_2 + 2\ R_1\ R_1\ R_2\ r_2 + 2\ R_1\ r_1\ r_2\ r_2 + 2\ r_1\ r_1\ R_2\ r_2 + 4\ R_1\ r_1\ R_2\ r_2$

The appearance and mode of inheritance in these 9 classes are given in the following table :—

	Appearance of grain in F_2.	Grain colour in F_3.
$R_1\ R_1\ R_2\ R_2$	red	red, uniform in tone.
$r_1\ r_1\ r_2\ r_2$	white	white, uniform.
$R_1\ R_1\ r_2\ r_2$	red	red, uniform in tone.
$r_1\ r_1\ R_2\ R_2$	red	red, uniform in tone.
$R_1\ r_1\ R_2\ R_2$	red	all red but not uniform.
$R_1\ R_1\ R_2\ r_2$	red	all red but not uniform.
$R_1\ r_1\ r_2\ r_2$	red	red and white in the ratio of 3 : 1.
$r_1\ r_1\ R_2\ r_2$	red	red and white in the ratio of 3 : 1.
$R_1\ r_1\ R_2\ r_2$	red	red and white in the ratio of 15 : 1.

PLATE 1



THE DISTRIBUTION OF RED TONES IN THE SECOND GENERATION

As mentioned above the fact that the two red factors both produce a red colour makes the identification of these various classes impossible. Nevertheless it was found possible to isolate the two factors. In order to assist in the analysis of the F_2 it was decided to form a set of arbitrary standards by selecting all the tones of red occurring in this generation and to assign all the plants to classes represented by these standards. Twelve definite shades of red were obtained which covered the whole range of tones. In appearance standards 1, 2, 3, were a very pale yellowish red passing by degrees to the full red of 8, 9, 10, 11 and 12. Although grain belonging to standard 1 can always be distinguished with certainty from white grain, nevertheless the colour is so faint that it is more yellow than red.

In classifying the F_2 generation the grain of the twelve standards was placed in watch glasses on white paper in a good north light and the grains of the remaining F_2 plants were matched singly and their respective places in the series determined.

The distribution of the F_2 plants as regards the tone of colour of the red grained individuals is given in the following table and again graphically in Plate I. The red curve is compounded of the three single curves given by three crosses.—

Cross.	No. of plants.	Red Standards.											
		1	2	3	4	5	6	7	8	9	10	11	12
Punjab Type 9												×	
F_1 of all crosses							×						
Punjab Type 9 × Punjab Type 16.	594	8	21	98	107	91	102	46	22	21	15	24	3
Punjab Type 9 × Moz. white.	705	9	34	86	178	109	70	70	54	20	15	13	3
Punjab Type 9 × Punjab Type 25.	954	13	27	137	120	184	78	105	68	96	20	42	6
Total ...	2,253	30	82	321	405	384	250	221	144	137	50	79	12

It will be observed that in the graphic representation the twelve red tones have been assumed for the sake of convenience to differ from one another by an equal amount. This is probably not the case, but does not affect the argument. For all the crosses the numbers have been calculated for 500 plants in order to make the comparison of the curves easier.

The red grained parent, Punjab Type 9, was found to be identical with the eleventh standard and the F_1 in all cases was intermediate between standards 5 and 6. The bulk of the plants in the F_2 appear in the centre of the curve. The curves obtained from the individual crosses agree very fairly well with each other and with the compound curve, especially if the difficulty of matching these slightly varying shades of red be taken into account. All the observations on this question both in the F_2 and F_3 generations were carried out by the same observer in order to minimise the personal equation.

A large number of F_2 plants, representative of all the various tones of red in the series, were then sown singly seed by seed and the resulting harvest examined in the same manner as the F_2. By this examination it was possible to identify the two shades of red representing the two factors R_1 and R_2 and to isolate wheats which, in all probability, contain each factor singly. It was found that the F_3 cultures derived from F_2 plants with grain belonging to the classes represented by standards 1 and 2 in all cases gave a ratio of 3 red grained to 1 white grained plant, the darkest red tone obtained being never higher than 5. The F_2 plants represented by standards 3 and 4 also gave the 3 : 1, but in each case some plants bred true to red and gave uniform progeny with pale red grains. A few plants giving the same pale red uniform progeny were also derived from standard 5, but generally speaking after standard 4 there is a distinct change in the nature of the F_3 cultures. Ratios of 15 red grained to 1 white, were obtained from standard 5 as well as some with 3 red to 1 white, but in this case the red tones ranged as high as standard 9. It is clear that in the region of the curve, in which standards 3 and 4 occurred, one of the red factors was to be found and this was represented by the pale constant reds obtained. The pale red F_2 plants represented by standards 1 and 2 which gave the 3 : 1 ratio must have been heterozygotes of the pale red and white gametes. In a similar manner many uniform red plants occurred at 9 and a few at standard 8. These were a full red and represented the other red factor. The plants in standard 5 which gave the 3 : 1 ratio with red tones up to standard 9 must have been heterozygotes of the dark red and white factors. The reds which were not uniform were met

with from standard 5 onwards, some ranged from 3 to 11, others from 9 to 12, and these must have been heterozygotes containing both the red factors. Thus the two red factors in the original parent have been isolated, the pale red factor corresponding to standard 4 and the darker red to standard 9. When both are present a dark red grain is obtained corresponding to standard 11, the tone of the original parent. The five sets of the heterozygotes are always intermediate in tone and with the four constant forms complete the series. The large preponderance of F_2 plants between standards 3 and 6 is easily explained by the occurrence at this point of the following forms—$R_1\ r_1\ R_2\ r_2$, $R_1\ R_1\ r_2\ r_2$, and $R_1\ R_1\ R_2\ r_2$. It will be seen that secondary maxima occur at 9 and 11 corresponding to the pure dark red factor and the two red factors combined.

Chaff Colour.

The investigations hitherto published on the inheritance of chaff colour are summed up by Tschermak in the 1910 edition of *Die Züchtung der land. Kulturpflanzen.*

In the five crosses we have made between red and white chaffed wheats, the results have been similar, and in all cases, after an intermediate F_1 generation, simple splitting in the ratio of 3 red to 1 white was obtained in the F_2. The results of the examination of 4,722 plants belonging to these five crosses are given in the following table :—

Table XII.

The F_2 generation of crosses between red and white chaffed parents.

Cross.		No. of plants.	Chaff Colour. Red.	White.	Ratio.
A 88 ♀ × Pusa 22 ♂	(1)	168	120	48	2·5 : 1
,, ,,	(2)	247	193	54	3·6 : 1
,, ,,	(3)	258	188	70	2·7 : 1
Pusa 22 ♀ × A 88	(4)	117	83	34	2·4 : 1
,,	(5)	196	145	51	2·8 : 1
Total.		986	729	257	2·8 : 1
Expectation			*739·5*	*246·5*	

TABLE XII—*continued.*

The F_2 generation of crosses between red and white chaffed parents—continued.

CROSS.		No. of plants.	CHAFF COLOUR. Red.	White.	Ratio.
B XI 77 ♀ × HI_2 ♂	(1)	194	151	43	3·5 : 1
,, ,,	(2)	227	175	52	3·4 : 1
,, ,,	(3)	233	190	43	4·4 : 1
HI_2 ♀ × BXI_{77} ♂	(5)	253	189	64	2·9 : 1
TOTAL		907	705	202	3·5 : 1
Expectation			*680·25*	*226·75*	
American Club ♀ × Pusa 4 ♂	(1)	156	120	36	3·3 : 1
,, ,,	(2)	177	136	41	3·3 : 1
,, ,,	(3)	195	146	49	3·0 : 1
,, ,,	(4)	124	95	29	3·3 : 1
,, ,,	(5)	192	139	53	2·6 : 1
,, ,,	(6)	216	164	52	3·1 : 1
TOTAL		1,060	800	260	3·1 : 1
Expectation			*795*	*265*	
Punjab Type 9 (α) ♀ × HII_4 ♂	(1)	137	106	31	3·4 : 1
,, ,,	(2)	189	130	59	2·2 : 1
,, ,,	(3)	185	138	47	2·9 : 1
H II_4 ♀ × Punjab Type 9 (α) ♂	(4)	117	87	30	2·9 : 1
,, ,,	(5)	176	134	42	3·2 : 1
TOTAL		804	595	209	2·8 : 1
Expectation			*603*	*201*	
Punjab Type 9 (γ) ♀ × Punjab Type 13 ♂		965	741	224	3·3 :
Expectation			*723·75*	*241·25*	

IV. THE PRESENCE AND ABSENCE OF AWNS.

The inheritance of awns in wheat has been investigated by several observers and the results obtained are to be found in von Tschermak's summary in *Die Züchtung*, which has been referred to under chaff colour. Biffen, Wilson, Schribaux and von Tschermak found that the beardless condition was dominant and that the F_2 generation was composed of bearded and beardless plants in the simple ratio 3 : 1. In some cases the ratio fully bearded to half bearded and beardless in this generation was 1 : 2 : 1. Nilsson-Ehle found however that the beardless condition was not absolutely dominant. Von Tschermak observed in two cases in crossing a bearded and beardless wheat that the bearded condition was entirely lost, while Rimpau and Spielmann on crossing two beardless wheats obtained in the F_2 a few bearded forms which bred true. Saunders[1] in 1906 combated the statement that the first generation between a beardless and a bearded wheat is always beardless, and maintained that the amount of bearding in the F_1 varies with the wheats used. In the F_2 a series of forms, which defied classification, was obtained. Apparently the subject was not further investigated as no details appear to have been published since.

In our investigations at Pusa with Indian wheats the inheritance of the fully awned character has not been simple. In crosses between bearded and beardless wheats two very distinct phenomena have been observed. In one series, the plants in the F_1 were distinctly intermediate and were half bearded, while in the other only very short tips to the glumes occurred. These differences in the F_1 were correlated with differences in the beardless parents. In the first case these had short tips to the

[1] Saunders, *Report of the Third International Conference 1906 on Genetics*, London, 1907, p. 370.

glumes, while in the second they were absolutely beardless. In the following paragraphs these two classes are dealt with separately.

The half bearded F_1 generation occurred in four crosses between bearded and beardless wheats and the results (Plate II) differ entirely from those illustrated by Biffen and Wilson in Vol. 1 of the *Journal of Agricultural Science*. The four crosses with an intermediate F_1 all broke up in the F_2 into fully bearded, half bearded like the F_1 and plants with tipped glumes in the ratio 1 : 2 : 1. There was no difficulty in distinguishing these classes which were very distinct the one from the other. The details relating to the 2,836 F_2 plants of these four crosses are given in the following table :—

Table XIII.

The F_2 generation of crosses between bearded and tipped parents.

Cross.		F_2 Generation. No. of Plants.	Bearded.	Intermediate.	Tipped.	Ratio.
BXI 77 ♀ × HI_2 ♂	(1)	194	47	105	42	1·1 : 2·5 : 1
,, ,,	(2)	227	67	113	47	1·4 : 2·4 : 1
,, ,,	(3)	233	52	116	65	·8 : 1·8 : 1
HI_2 ♀ × BXI 77 ♂	(5)	253	62	123	68	·9 : 1·8 : 1
Total		907	228	457	222	1 : 2·1 : 1
Expectation			*226·75*	*453·5*	*226·75*	
Punjab Type 9 (*a*) ♀ × HII_4 ♂	(1)	137	35	71	31	1·1 : 2·3 : 1
,, ,,	(2)	190	54	89	47	1·1 : 1·9 : 1
,, ,,	(3)	185	46	87	52	·9 : 1·7 : 1
,, ,,	(4)	117	32	55	30	1·1 : 1·8 : 1
HII_4 ♀ × Punjab Type 9 (*a*) ♂	(5)	175	48	89	38	1·3 : 2·3 : 1
Total		804	215	391	198	1·1 : 2·0 : 1
Expectation			*201*	*402*	*201*	
Punjab Type 9 ♀ × Punjab Type 25 ♂		1,022	244	528	250	1 : 2·1 : 1
Expectation			*255·5*	*511*	*255·5*	
American Club ♀ × Pusa 6 ♂	(1)	133	42	56	35	1·2 : 1·6 : 1
,, ,,	(2)	215	62	98	55	1·1 : 1·8 : 1
,, ,,	(3)	178	58	81	39	1·5 : 2·1 : 1
,, ,,	(4)	97	24	49	24	1·0 : 2·0 : 1
,, ,,	(5)	179	47	85	47	1·0 : 1·8 : 1
,, ,,	(6)	201	60	90	51	1·2 : 1·8 : 1
Total		1,003	293	459	251	1·2 : 1·8 : 1
Expectation			*250·75*	*501·5*	*250·75*	

Punjab Type 9.

H II.

Parents.

First Generation.

Fully bearded.

Intermediate.

Tipped.

Second Generation.

THE RESULT OF CROSSING BEARDED AND TIPPED WHEATS

In one of these crosses (Punjab Type 9 × Punjab Type 25), a large number of the three kinds of F_2 plants were grown and the F_3 generation examined. All the fully bearded plants and those with tips bred true, while the half bearded plants again split up into fully bearded, half bearded and tipped plants in the ratio 1 : 2 : 1. The details relating to thirty-one of these cultures are given in the following table :—

Table XIV.

The F_3 generation of a cross between bearded and tipped parents.

Plant No.	Bearding in F_2 parent.	No. of plants in F_3.	Bearding in the F_3 Generation.			Ratio.
			Fully bearded.	Intermediate.	Tipped.	
10	Fully bearded	77	77	..	...	
31	do.	90	90	...	...	
218	do.	77	77	...	..	
233	do.	71	71	...	...	
319	do.	81	81	...	...	
459	do.	74	74	...	.	
470	do.	122	122	...	...	
499	do.	87	87	...	...	
611	do.	139	139	...	..	
649	do.	122	122	...	...	
924	do.	132	132	...	...	
65	Tipped	75	...	...	75	
138	do.	99	...	...	99	
509	do.	102	...	...	102	
566	do.	115	...	...	115	
582	do.	91	...	...	91	
787	do.	96	...	...	96	
853	do.	94	...	...	94	
940	do.	88	...	..	88	
1004	do.	113	...	...	113	
1026	do.	94	...	...	94	
1	Intermediate	60	16	26	18	
4	do.	49	15	27	7	
30	do.	93	21	49	23	
75	do.	86	19	41	26	
79	do.	62	14	27	21	
184	do.	63	18	33	12	
317	do.	83	17	43	23	
368	do.	70	15	31	24	
401	do.	90	29	38	23	
468	do.	77	19	42	16	
481	do.	66	15	34	17	
507	do.	70	17	35	18	
623	do.	51	12	28	11	
760 ×	do.	62	18	27	17	
803	do.	66	12	39	15	
818	do.	80	17	46	17	
863	do.	55	16	23	16	
911	do.	89	20	46	23	
973	do.	80	20	44	16	
990	do.	67	14	38	15	
	Total	1419	344	717	358	·96 : 2 : 1
	Expectation		*354·75*	*709·5*	*354·75*	

The crosses between bearded and beardless plants in which the F_1 generation was apparently beardless will now be considered.

This was observed in the following pure line crosses in which the bearded parent is placed first :—

1. American Club × Pusa 4.
2. Pusa 22 × A 88.

In both the beardless parents Pusa 4 and A 88 there was an entire absence of tips, and these parents could be described as absolutely beardless. In the second generation of these crosses a series of forms was produced which we have classed with difficulty as fully bearded, almost fully bearded, half bearded, forms with tips of varying length and beardless (Plate III). If all the variously bearded and tipped plants are classed as bearded, which would seem to be the most logical method, the ratio bearded to beardless obtained was 15 : 1 and the presence of two factors is indicated. Representatives of the various classes are now being grown in the F_3 and the full explanation, as well as the complete study of the F_2, will be dealt with next spring as soon as the plants are ripe. The details relating to the F_2 generation of these crosses are given in the following table :—

TABLE XV.

The F_2 generation of crosses between bearded and quite beardless parents.

CROSS.	No. of plants.	BEARDING IN THE F_2 GENERATION. Fully bearded.	Almost fully bearded.	Half bearded.	Tips of varying length.	Beardless.
American Club ♀ × Pusa 4 ♂ (1)	156	8	11	24	105	8
,, ,, (2)	176	12	11	27	113	13
,, ,, (3)	197	10	12	24	138	13
,, ,, (4)	124	6	9	14	84	11
,, ,, (5)	192	11	13	24	132	12
,, ,, (6)	216	11	14	22	155	14
TOTAL	1061	58	70	135	727	71
Ratio	...	·8	1	1·9	10·2	1
A 88 ♀ × Pusa 22 ♂ (1)	168	12	11	19	117	9
,, ,, (2)	247	18	11	28	173	17
,, ,, (3)	258	16	20	31	174	17
Pusa 22 ♀ × A 88 ♂ (4)	117	5	11	17	76	8
,, ,, (5)	196	10	12	29	133	12
TOTAL	986	61	65	124	673	63
Ratio		1	1	2	10·7	1

Pusa 22.

A 88.

Parents.

First Generation.

Fully bearded.

Nearly fully bearded.

Half bearded.

Long tips.

Short tips.

Beardless.

Second Generation.

THE RESULT OF CROSSING BEARDED AND BEARDLESS WHEATS.

The distinction between the above two kinds of inheritance in bearding is of great interest. In one case the simple Mendelian scheme is followed, but there is no question of dominance in the F_1 which is clearly intermediate. In all these cases however one of the parents is only beardless in the ordinary sense of the term, short tips to the glumes being present. In the other case the F_1 is almost beardless while in the F_2 the 15 : 1 ratio is obtained when all plants with beards, whatever may be their length, are separated from the absolutely beardless ones. Here, however, one of the parents is absolutely beardless.

In the following crosses the same bearded parent (American Club) occurs in both classes—

(1) American Club (bearded) × Pusa 6 (beardless) with the 1 : 2 : 1 ratio in the F_2.

(2) American Club (bearded) × Pusa 4 (beardless) gave the 15 : 1 ratio in the F_2.

Pusa 6 has short tips to the awns while Pusa 4 is absolutely beardless. This appears to indicate that in American Club two factors are present, a long and short factor, while both are absent in Pusa 4 and only the short factor is present in Pusa 6.

Before discussing the possible explanations of these phenomena the results of the other crosses made with bearded parents must be stated. In crosses between plants with slight tips to the awns and absolutely beardless parents the F_1 generation was intermediate and the F_2 gave fully tipped, intermediate and absolutely beardless plants in the ratio 1 : 2 : 1 and no difficulty was experienced in making the separation. Crosses between fully bearded parents gave similar offspring in the F_1 and again in the F_2. In crosses between tipped parents the F_1 and F_2 generations were alike and resembled the parents in having all the awns with tips of similar length. These results are given in the following table :—

TABLE XVI.

The F_2 generation of crosses between tipped and beardless parents.

CROSS.		No. of plants.	F_2 GENERATION. Fully Tipped.	Inter-mediate.	Beard-less.	Ratio.
Biffen's hybrid ♀ × Pusa 4 ♂	(2)	178	42	94	42	
,, ,,	(5)	221	49	129	43	
,, ,,	(6)	197	39	101	57	
TOTAL		596	130	324	142	·9 : 2·3 : 1
				454		
Biffen's hybrid ♀ × Pusa 4 ♂	(1)	158		113	45	
,, ,,	(3)	110		81	29	
,, ,,	(4)	115		91	24	
TOTAL of all 6 plants		979		739	240	3·07 : 1
Expectation				*734·25*	*244·75*	

TABLE XVII.

The F_2 generation of crosses between bearded parents.

CROSS.		No. of plants.	Nature of Progeny in F_2
American Club ♀ × Pusa 22 ♂	(1)	122	All fully bearded.
,, ,,	(2)	165	,, ,, ,,
,, ,,	(3)	192	,, ,, ,,
,, ,,	(4)	75	,, ,, ,,
,, ,,	(5)	147	,, ,, ,,
,, ,,	(6)	176	,, ,, ,,
TOTAL		877	,, ,, ,,
American Club ♀ × Pusa 23		137	All fully bearded.
Punjab Type 9 ♀ × Punjab Type 16 ♂		1188	,, ,, ,,
Punjab Type 9 ♀ × Moz. White ♂		1150	,, ,,
Punjab Type 9 ♀ × Punjab Type 13 ♂		965	,, ,, ,,

Table XVIII.

The F_2 generation of crosses between tipped parents.

Cross.	No. of plants.	Beardless.	Tipped.
Biffen's hybrid ♀ × Pusa 6 ♂ (3)	179	.....	179
,, ,, (6)	163	.....	163
Total	342		342

The complete explanation of these ratios in the F_2 and the isolation of the two factors concerned in the 15 : 1 ratio can only be arrived at after the F_3 generation of this latter cross has been grown and the results examined in detail. The simplest explanation appears to be that in the bearded parent two factors are present, one capable of producing short awns or tips only, the other resulting in fully bearded plants, while in the tipped parents the short factor only is present. On the presence and absence hypothesis, the results of the various crosses would be represented as follows: Assuming the fully bearded parent contains two factors B and T (B representing the long and T the short factor), the tipped plants contain only one factor T, while the absolutely beardless plants contain neither, then—

(1) Fully bearded wheats would be represented by B B T T.
(2) Plants with tips only would be represented by b b T T.
(3) Absolutely beardless plants would be represented by b b t t.

The various crosses described above would then be represented as follows:—

1. Fully bearded (BBTT) × tipped (bbTT) would give in the F_1 BbTT and in the F_2 1 BBTT + 2BbTT + 1 bbTT.
2. Fully bearded (BBTT) × beardless (bbtt) would give BbTt in the F_1 and the F_2 would be represented by the formula:—

   BBTT + 4 BbTt + 2 BbTT + 2 BBTt + bbTT + 2 bbTt + BBtt + 2 Bbtt + bbtt.
3. Tipped (bbTT) × beardless (bbtt) would give in the F_1 bbTt and in the F_2 bbTT + 2 bbTt + bbtt.

4. Bearded (BBTT) × Bearded (BBTT) would give BBTT in both the F_1, and the F_2.
5. Tipped (bbTT) × Tipped (bbTT) would give the same bbTT in both the F_1 and the F_2.

Whether the above explanation, in which the bearded parent contains two factors, will hold or not will be proved by the study of the F_3 generation. Another explanation has been suggested by von Tschermak, namely, the presence of a restraining factor in the beardless parent. This, however, does not seem to fit the facts so easily as that put forward by ourselves, and in this connection it should be noted that the sharp distinction here drawn between absolutely beardless and so-called beardless plants with short tips does not seem to have been made before. It appears that tipped plants have been regarded as beardless in most of the European work and that crosses with really beardless plants have not been made. In our Indian collection most of the " beardless " plants are tipped and absolutely beardless plants, which are the best analysers for the study of the bearded character, are rare.

Colour of the Awns.

In many of the Indian wheats the awns are black, whenever the wheats are fully developed. If, however, premature ripening takes place, this colour is not developed. In one cross between a black and a white awned wheat the inheritance of black awns in the F_2 was determined. The black awns prevailed in the F_1 and in the F_2 the ratio of black awns to white was 3·45 to 1, the actual numbers being 466 black and 135 white. It was not possible to separate the fully black awned plants from the intermediates, but the occurrence of these two classes was evident. The parents used were Punjab Type 9 (black awned), and Punjab Type 16 (white awned).

V. OTHER CHARACTERS.

In addition to the investigations on the inheritance of felted chaff, red grain colour and the bearding of wheat, some other characters have been studied, three of which are referred to briefly in this section. The complete investigations on these points will be dealt with in later papers. The characters in question are the consistency of the grain, the shattering of the ear and standing power.

Consistency of the Grain.

The results of our investigations on the influence of the environment on the consistency of wheat are now being published. It has been found that wheats can be divided into three groups as regards this matter. In the majority of Indian wheats, whether soft or translucent, this character is greatly influenced by the environment, and soft wheats are easily changed to translucent and *vice versâ*. A few translucent wheats, however, have a decided tendency to remain translucent under all conditions, while some soft wheats have so far remained soft no matter how or where they are grown. In one of the crosses at Pusa one of these constant soft white wheats was crossed with a strong translucent amber wheat and the segregation was so clear in the F_2 that counts were made. The F_1 was intermediate and the F_2 split sharply into soft, semi-translucent and translucent in the ratio 1 : 2 : 1. It will be seen from the following table that the results obtained are practically identical with expectation :—

TABLE XIX.

The F_2 generation of a cross between translucent and soft grained parents.

CROSS.	No. of plants.	CONSISTENCY.			Ratio.
		Soft.	Semi-translu-cent.	Translu-cent.	
A 88 ♀ × Pusa 22 ♂ (1)	167	39	82	46	1 : 2·1 : 1·2
,, ,, (2)	247	58	132	57	1 : 2·3 : 1
,, ,, (3)	256	67	125	64	1 : 1·9 :
Pusa 22 ♀ × A 88 ♂ (5)	196	43	108	45	1 : 2·5 : 1
TOTAL ...	866	207	447	212	1 : 2·1 : 1
Expectation		*216·5*	*433*	*216·5*	

TABLE XX.

The Nitrogen content in the F_2 generation of a cross between translucent and soft grained parents.

	Consistency.	Nitrogen percentage.
A 88	Soft	2·21
Pusa 22	Translucent	2·51
A 88 × Pusa 22 F_2 1	Soft	2·32
,, ,, 2	,,	2·42
,, ,, 3	,,	2·29
,, ,, 4	,,	2·43
,, ,, 5	,,	2·32
,, ,, 6	,,	2·07
A 88 × Pusa 22 F_2 7	Semi-translucent	2·31
,, ,, 8	,,	2·32
,, ,, 9	,,	2·57
,, ,, 10	,,	2·35
,, ,, 11	,,	2·53
,, ,, 12	,,	2·30
A 88 × Pusa 22 F_2 13	Translucent	2·50
,, ,, 14	,,	2·78
,, ,, 15	,,	2·36
,, ,, 16	,,	2·47
,, ,, 17	,,	2·35
,, ,, 18	,,	2·43

A similar sharp segregation was observed in some of the crosses made at Pusa in 1906, but the figures were not published as one of the parents used was not a pure line.

Some nitrogen determinations[1] were made of the various classes in the F_2, and these are given in the table above. It will be seen that both parents are high in nitrogen, and that in the second generation there is no connection between translucency and high nitrogen content, but that both these characters are inherited independently. Plants with low and high nitrogen occur in all the classes. It is proposed to study this cross in detail from the point of view of the inheritance of strength and free-milling qualities.

Shattering of the Ear.

In India, one of the important characters of wheat from the economic standpoint is the power of holding the grain in the ear when the wheat is ripe. At harvest time the temperature is high, the air exceedingly dry and high winds are common. Moreover, it is the custom to allow the wheat to become dead ripe before it is cut, and owing to scarcity of labour at harvest time it often remains standing in the fields long after it is ripe. Under these circumstances many wheats drop their grain and a great loss of wheat results. In the improvement of Indian wheat any tendency to shed grain is a fatal defect in a new wheat, and several otherwise excellent types have had to be discarded by us on this account. In one of our crosses a distinct segregation in the F_2 was noticed as regards the shattering of the ear, and the 15 : 1 ratio was perfectly distinct. Two factors must therefore have been present, one of which it is likely to be found in Pusa 6 as this line has a tendency to shed its grain, but the shattering of many plants in the F_2 was much greater than in Pusa 6.

The details relating to the F_2 of the cross in question are given in the following table :—

Name of cross.	No. of plants.	Non-shattering.	Shattering.	Ratio.
American Club × Pusa 6 (2)	215	12	203	1 : 16·9

[1] We are indebted to Dr. Leather, Imperial Agricultural Chemist, for these nitrogen determinations.

Standing Power.

Perhaps the most important character in the improvement of Indian wheat at the present time is standing power. Now that it has been shown to be possible in the plains of India to raise crops exceeding forty bushels to the acre, it is clear that good standing power is essential to carry this weight of grain and for the crop to remain erect after the storms of wind and rain which often occur after the plants are in ear. Most of the Indian wheats have very weak straw, only suitable for carrying crops of about twenty bushels to the acre. In improving wheat production, therefore, both as regards methods of cultivation and quality, great attention has to be paid to standing power. Standing power appears to be due to at least two factors, first to strong straw, which is generally associated with very erect ears, and, secondly, to what may be called power to form a strong root system. In one of our crosses a parent with strong straw but inferior rooting power (A 88) was crossed with a wheat with weak straw but which rooted well (Pusa 22) and the F_2 plants were examined in detail. All combinations of these factors were evident in the F_2—well-rooted wheats with strong straw, well-rooted wheats with weak straw, wheats with strong straw and inferior rooting power as well as some which had neither good straw nor good rooting power. Careful records were kept of individual plants, but in a character like this it is not possible to secure accurate counts. This evidence of distinct segregation renders it likely, however, that it will be an easy matter to secure wheats with strong straw and good rooting power and to increase the standing power of the Indian wheats very considerably.

VI. SUMMARY AND CONCLUSIONS.

The results obtained in these investigations may be summed up as follows :—

1. The hairs on the chaff of felted wheats vary considerably in length and density and one or more kinds of hairs may be present in the same wheat. In all the hybridization experiments carried out so far, each kind of hair has proved to be due to a single factor, and these factors are inherited independently of one another. The number of kinds of hairs and consequently of gametic factors involved in the felting of wheats is probably large. All of the Indian macaroni wheats examined up to the present and also all densely felted wheats have two kinds of hairs.

2. The red colour of the grain of wheat may be due to the presence of one, two or three factors which are inherited independently of each other. Each is capable of producing a red colouration, but the shade of red thus produced varies. It is possible to isolate from a cross between a red wheat with a multiple grain colour and a white wheat, wheats possessing grains of intermediate shades of red which bred true at once. The effect of the two red factors in Punjab Type 9 is cumulative, and the colour of the grain of this wheat is deeper than that produced by either of the two factors singly. Only one factor was found to occur in all the crosses between red and white chaffed wheats which after an intermediate F_1 gave the usual 1 : 2 : 1 ratio in the F_2.

3. The existence of at least two factors in the bearding of wheats has been demonstrated, and it has been shown that a sharp distinction must be drawn in the future between wheats which are absolutely beardless, and those with very short awns or tips. The usual practice of classing all wheats with awns not longer than one quarter of an inch or so as beardless is misleading.

4. The black colour of the awns prevailed in the cross Punjab Type 9 × Mozaffarnagar white and segregation in the F_2 of three black to one white awned plant was obtained.

5. On crossing a constant soft wheat with a translucent one, distinct segregation into soft, intermediate and translucent wheats was obtained in the Mendelian ratio of 1 : 2 : 1. This segregation was independent of the nitrogen percentage.

6. In the shattering of the ear two factors appear to be involved and distinct segregation with intensification was observed in the F_2.

7. Segregation was also observed in a cross between a weak strawed well rooted wheat and a strong strawed wheat with inferior rooting capacity. All possible combinations were found, and the prospect of obtaining a well rooted strong strawed wheat in the future seems favourable.

8. In none of the crosses was there any indication of dominance in the first generation, which in all cases proved to be intermediate.

From the general standpoint of the improvement of crops the more modern investigations on hybridization are not without interest. In concluding this account an attempt will be made to indicate the bearing of these investigations on the wider aspects of plant breeding work conducted with the object of obtaining better staples than those now cultivated. At the present time in many countries there is a considerable amount of state-aided effort devoted to the advancement of agriculture, and one of the chief activities of the various Agricultural Departments is concerned with plant breeding and selection.

1. The Preservation of Pure Lines.

The most modern investigations on hybridization confirm the necessity of starting all plant breeding work from pure lines, the

characters of which have been studied adequately. In the present state of knowledge, this is undoubtedly the best material available for the purpose and, consequently, the preservation of the pure lines for the benefit of future workers becomes an important matter. This is particularly so in countries like India where reliable seed merchants do not exist, and where it is practically impossible to procure varieties of crops even botanically pure. Before hybridization work can be begun in India, it is necessary to make surveys of the particular crops studied and to separate them not only into botanical varieties and finally into pure lines but also to determine with precision all the characters of the pure lines themselves. All this preliminary work necessarily involves the expenditure of considerable time and money. As hybridization work proceeds more and more, pure lines of known gametic constitution will become, as it were, accumulated at the various stations, and the proper preservation of this material is an important matter, and becomes a valuable asset of the Agricultural Department concerned. It is important that it should not be lost and that it should be readily available for future workers in a manner somewhat similar to the way in which, at research centres, libraries of books are handed down to posterity.

The preservation and exchange of pure lines, the gametic constitution of which has been proved, might easily become of very general importance. There is little doubt that hybridization work will, in the future, become in each country more and more restricted to a few centres, and it is very probable that the material of one country may be of use to the workers at centres in other countries. Thus there may very easily be useful exchanges of pure lines in Northern Europe and again in North America. The whole subject of the best means of preserving pure lines of economic plants of known gametic constitution is one which might well be taken up by the next International Conference on Genetics or by the International Association of Botanists.

II. Plant Breeding Stations.

The complexity of such apparently simple characters in wheat

as those dealt with in the present paper leaves little doubt that the number of factors involved in characters of economic importance such as strength of flour, rust resistance and standing power are equally great. This in turn renders the isolation of new kinds which bred true in all respects, from the progeny of a cross, a matter of greater labour and longer time than was at one period suspected. In addition many of these characters are subject to the influence of environment, so that both the study of inheritance and the work of breeding improved varieties becomes increasingly difficult. If progress is to be made in the elucidation of the laws of inheritance on the one hand and in the production of improved crops on the other, it seems difficult to resist the conclusion that there can be little or no progress in either direction unless the work is organised in such a manner that it is restricted to a few centres adequately equipped. The publication of the early researches on inheritance, which followed closely on the rediscovery of Mendel's law, undoubtedly stimulated a large amount of hybridization work at the Agricultural Experiment Stations and was the means of raising expectations that the improvement of crops was a simple matter and might be accomplished in a very short period. As a consequence, plant breeding was started at stations as an addition to an already overloaded programme and the result has been to flood the literature with a mass of superficial results of no permanent value. Whenever plant breeding has been done with thoroughness and on a sufficiently large scale, it has invariably been found that the inheritance of characters is by no means such a simple matter as was first supposed, and the investigations conducted at such centres as Svalöf explain why it is that the numerous attempts at plant improvement made at the Agricultural Experiment Stations have not led to any very striking results. There is no doubt that plant breeding work is useless unless it is carried out on a large scale and with great thoroughness. This in turn can only be done effectively at Experiment Stations at which this work is made the chief item of the programme. It would be better, therefore, for each country to maintain a few good plant improvement stations than to carry on superficial investigations at many centres.

III. The Basis of Selection.

The results obtained in the present paper have a considerable bearing on selection. It has been shown in wheat that characters, which appear at first sight to be simple, are in reality made up of several factors, each inherited independently of one another. The total number of factors in this crop will no doubt be found to be considerable. Natural cross-fertilization has been shown to be much commoner than was at one time suspected, and this supplies the means by which these factors can combine together to form a very large number of wheats, differing from each other by small amounts. The known complexity of botanical varieties in wheat is at once explained by the interplay between the numerous factors rendered possible by natural crossing. Consequently, the wheats of any region and especially those of a country like India, in which agriculture has been practised from time immemorial, supply material, which may well turn out to be a veritable gold mine, for the exercise of systematic schemes of selection. The careful comparison of the offspring of single plants may yield results of great value to the country. A similar state of affairs appears, from our observations in India, to obtain in several other crops in which self-fertilization is the rule. The comparison of the pure lines of these self-fertilized crops offers a line of work which may prove to be of the very greatest importance in agriculture and is moreover much simpler than hybridization investigations. The only difficulties involved are those relating to the interpretation of the results of the field trials in deciding whether or not an improvement has really been obtained.

These results also concern the question of the improvement of plants in which crossing is common. Here there is little doubt also that numerous factors are involved. These, however, have crossed so much among themselves that there has been no opportunity for the production of pure lines, so that the crops are a network of freely intercrossing forms. A large amount of systematic selection, extending over a considerable period, is therefore necessary before material, in any sense approximating to pure lines, can be obtained. While, therefore, the question of selection in self-fertilized crops is

seen to be established more firmly as a result of recent work on hybridization, the difficulties in applying this process with success to cross-fertilized crops appear to be very much greater. Further, the question of the maintenance of the vigour of these latter crops, when grown in pure culture and when crossing is prevented, is a subject which, up to the present, has not received a very large amount of attention.

QUETTA,
SEP. 16TH, 1912.

VII. DESCRIPTION OF THE WHEATS USED IN THE HYBRIDIZATION EXPERIMENTS.

TRITICUM VULGARE, VILL.

1. *Punjab Type* 9[1].—Ears bearded; awns stiff, stout, rather short, black but lose their colour very easily; glumes sharply keeled to the base, chaff densely felted, greyish white; grain very dark red.
2. *Punjab Type* 13.—Ears bearded, awned, red; chaff smooth, light red; grain red.
3. *Punjab Type* 16.—Ears bearded; chaff smooth, white; grain white, small.
4. *Punjab Type* 25.—Ears beardless, but with very short awns (tipped); chaff smooth, yellowish white, shiny; grain white, large.
5. *Mozaffarnagar White.*—Ears bearded; chaff smooth white; grain white.
6. *H* I_2.—Ears beardless, but with very short awns (tipped); chaff smooth, red; grain red.
7. *H* II_4.—Ears beardless, but with well marked short awns (tipped); chaff smooth, red; grain white.
8. *H* III_8.—Ears beardless, but with very short awns (tipped); chaff smooth, white; grain red.
9. *B XI* 77.—A pure line from Bengal class VII. Ears bearded; chaff felted, white; grain white.
10. *A* 88.—Ears quite beardless, club-shaped at apex; chaff smooth, red; grain white, soft; straw very strong and stout.
11. *Pusa* 4.—Ears quite beardless; chaff lightly felted, white; grain white.
12. *Pusa* 6.—Ears beardless, but with short awns (markedly tipped); chaff smooth, red; grain white.
13. *Pusa* 22.—Ears bearded; chaff smooth, white; grain amber, very translucent; straw weak and thin.
14. *Pusa* 23.—Ears bearded; chaff smooth, white; grain red.
15. *Biffen's hybrid.*—Ears beardless, but with very short awns; chaff smooth, white; grain red.

TRITICUM DURUM, DESF.

16. *Pusa* 20.—Awns long, easily shed, black but lose their black colour very easily; chaff felted, light red; grain amber.

TRITICUM COMPACTUM, HOST.

17. *American Club.*—Ears bearded with stiff awns; chaff smooth, red; grain red.

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[1] Howard and Howard, *Wheat in India*, Calcutta, 1909.